

Weeds, seeds, and buds—opportunities and systems for dormancy investigations

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Dormancy is a critical factor for the survival and persistence of weedy species. Contemporary approaches can be used to identify genes that regulate dormancy directly or indirectly to elucidate key mechanisms, signals, and pathways. Several domesticated plant species have been used as model systems to mark quantitative trait loci (QTL) that affect dormancy in seeds and vegetative propagules directly. A few weedy species have also been used to mark QTL and to determine dormancy genes using microarray analysis. Given the number of serious weeds worldwide and the role that dormancy plays in their persistence, developing fundamental knowledge on dormancy is an important step toward developing new strategies for weed management. This paper describes current research and outlines some weeds that might be candidates for dormancy investigations using molecular genetic and genomics approaches. An underlying theme in the selection of weeds for dormancy investigations is their relation to crop species and the ability to adapt existing resources to investigate dormancy in weedy plants.

Nomenclature: Canada thistle, *Cirsium arvense* (L.) Scop. CIRAR; green foxtail, *Setaria viridis* (L.) Beauv. SETVI; horsenettle, *Solanum carolinense* L. SOLCA; johnsongrass, *Sorghum halepense* (L.) Pers. SORHA; Jerusalem artichoke, *Helianthus tuberosus* L. HELTU; jointed goatgrass, *Aegilops cylindrica* Desf. AEGCY; leafy spurge, *Euphorbia esula* L. EPHE; prickly lettuce, *Lactuca serriola* L. LACSE; purple nutsedge, *Cyperus rotundus* L. CYPRO; wild mustard, *Brassica kaber* (DC.) L. C. Wheeler SINAR; wild oat, *Avena fatua* L. AVEFA; yellow nutsedge, *Cyperus esculentus* L. CYPES; Arabidopsis or mouse-ear cress, *Arabidopsis thaliana* L.; Asian wild rice, *Oryza rufipogon* Griff.; foxtail millet, *Setaria italica* (L.) P. Beauv.; oat, *Avena sativa* L.; potato, *Solanum tuberosum* L.; rice, *Oryza sativa* L.; sorghum, *Sorghum bicolor* (L.) Moench; wheat, *Triticum aestivum* L.

Key words: Developmental arrest, plant development, vegetative propagules.

Baker (1974) described 12 characteristics that might be expected in an ideal weed. Several of these characteristics deal directly or indirectly with dormancy or arrested growth and development. The first characteristic, “germination requirements fulfilled in many environments,” is due in part to genetic factors for dormancy and their interaction with the environment. The second characteristic, “discontinuous germination (internally controlled) and great longevity of seeds,” deals directly with seed dormancy and longevity of seeds in the soil. The 10th characteristic, “if a perennial has vigorous vegetative reproduction or regeneration from fragments,” suggests regeneration of whole plants from meristematic tissue. These meristems are generally referred to as buds and are associated with roots, rhizomes, stolons, or tubers of perennial weeds. Depending on the plant’s phenologic stage and various external factors, buds can be in various states of growth and development, including innate dormancy and correlative inhibition (Nissen and Foley 1987).

Dormancy is an adaptive trait that promotes the survival of many organisms (Viémond and Crabbé 2000). From a weed science perspective, dormancy optimizes the distribution of shoot emergence over time, and therefore is a key factor that allows weeds to escape control by chemical, cultural, mechanical, and biological measures. Because dormancy plays an important role in the population dynamics

of weeds, fundamental knowledge about mechanisms regulating dormancy is needed to solve problems in weed management. In the past several years, researchers from a variety of disciplines have begun using molecular genetic and genomic approaches to elucidate dormancy mechanisms. In this paper, I outline some useful and potentially useful systems for dormancy investigations and suggest opportunities for investigating dormancy in seeds and vegetative propagules of weeds.

Model Plant Systems for Dormancy Investigations

Arabidopsis

Arabidopsis is widely accepted as a model system for research in plant developmental biology (Meyerowitz 1994). Arabidopsis is the most advanced system for investigating many plant processes including the molecular genetic basis for seed dormancy and longevity (Bentsink et al. 2000; Koornneef et al. 2000; Koornneef and Karssen 1994). Arabidopsis is a relatively small plant that is capable of producing mature seeds in as little as 4 to 6 wk. The small stature and short generation time conserve limited greenhouse space and facilitate research progress to meet the constraints of 3-yr research grant cycles. A broad array of germplasms with different levels of germinability are available

TABLE 1. List of technical nomenclature.^a

Term	Definition
cDNA library	A collection of cDNA clones derived from one mRNA preparation
Complementary (c)DNA	DNA molecule that is synthesized from an mRNA template
DNA microarray	cDNA fragments arrayed onto a small chip for genome-scale analysis of gene expression patterns
Ecotype	A locally adapted variant of a plant, differing genetically from other ecotypes
Epistasis	The condition where one gene suppresses the expression of another gene. The gene that does the suppressing is called the epistatic gene
Expressed sequence tag (EST)	A short (200 to 500 bp) DNA sequence, derived from a cDNA
Genomic library	An unordered collection of clones made from a set of overlapping DNA fragments representing an organism's entire genome
Linkage map	A map of the relative positions of genetic loci on a chromosome, determined on the basis of how often the loci are inherited together
Mapping clone	cDNA and genomic clones used to construct a genetic, linkage, or physical map of an organism
Mapping population/lines	The group of related organisms used to analyze linkage and crossover frequencies to construct a genetic map
Quantitative trait locus (QTL)	A segment of the chromosome associated with the expression of an individual allele controlling a quantitative trait
QTL analysis	Scanning the genome and marking chromosomal regions containing polygenes governing a quantitative trait
Recombinant inbred (RI) lines	Genetic lines produced by inbreeding the progeny of an F ₂ derived from two well-established progenitor inbreds over a number of generations
T-DNA tagged lines	Plants transformed with transfer (T)-DNA and used in insertional mutagenesis or activation tagging, a gene overexpression screen in which transcriptional enhancers such as the viral 35S promoter/selectable marker are randomly inserted in the genome

^a Many contemporary life science terms are defined in The BioTech - Life Science Dictionary and in Human Genome Project - Genome Glossary available at <http://biotech.icmb.utexas.edu/search/dict-search.phtml> and at http://www.ornl.gov/TechResources/Human_Genome/glossary/glossary.html#genomiclibrary, respectively. Accessed August 27, 2001.

from repositories such as the Arabidopsis Biological Resources Center and the Nottingham Arabidopsis Seedstock Center (Anonymous 2001a, 2001b). The germplasm in these repositories consists of ecotypes, recombinant inbred lines, mapping lines, T-DNA tagged lines, and mutant stocks (see Table 1 for definitions) which have been used to examine dormancy, hormone action, and phytochrome response. In addition, mapping clones, libraries, and individual clones from libraries are publically available from individual scientists and DNA stock centers (Anonymous 2001a). The Arabidopsis genome is relatively small (130 Mbp), which facilitates map-based cloning of genes and sequencing the entire genome (Arumuganathan and Earle 1991). The elucidation of the full genome sequence of Arabidopsis, with its estimated 25,498 genes, is a milestone in plant science research (Kaul et al. 2000). The completed sequencing project opens new doors for everyone conducting research on plants, including weedy plants. One minor drawback of using Arabidopsis for seed dormancy investigations is its small seed size. For example, if one seeks to investigate embryo dormancy, excising a large number of embryos or embryonic axes would be more difficult with Arabidopsis than with a larger-seeded species.

An Arabidopsis recombinant inbred line population, developed from a cross between the strongly dormant 'Cape Verde Island' (Cvi) and less dormant 'Landsberg erecta' (Ler) accessions (Alonso-Blanco et al. 1998), was used to identify seven chromosomal regions or quantitative trait loci (QTL) that affect germinability (Koornneef et al. 2000). One region in chromosome 5 contains a major QTL for this trait

and near-isogenic lines are being used to clone this QTL (Koornneef et al. 2000). Developing near-isogenic lines where a single genomic segment contains the QTL in an otherwise uniform genetic background can reduce the complexity of a polygenic trait by causing most of the phenotypic variance for the trait to be governed by a single gene in a particular line. This strategy allows Mendelian resolution of a QTL. At the February 2001 Weed Science Society of America symposium on Dormancy in Seeds and Vegetative Propagules, Dr. Maarten Koornneef reported that his group had identified a contig, or a contiguous sequence of approximately 10 genes, from a bacterial artificial chromosome (BAC) clone that contains the putative Arabidopsis QTL on chromosome 5. If their subsequent work to clone and characterize the gene(s) involved is successful, this could be the first incidence that a QTL associated with germinability is cloned using map-based procedures. Whereas various genes that affect germinability of Arabidopsis seeds have been cloned and characterized before (Giraudat et al. 1992; Sun et al. 1992), none of these genes has been shown by QTL analysis to regulate germinability directly.

Rice

Oryza sativa L., known as rice, red rice, weedy or wild-like rice, is collectively an important crop, a weed, and a nondomesticated plant. Rice is a monocot and an important model system for cereal grain species (Yuan et al. 2001). Rice breeders are interested in genes that impart low and predictable levels of hull-, pericarp/testa-, or embryo-im-

posed dormancy to prevent preharvest sprouting (Lin et al. 1998). Plant physiologists study dormancy in red rice to understand mechanisms for dormancy and determine methods to induce uniform germination (Cohn 2002). Because rice is an important crop, many genotypes and genetic tools are available (Anonymous 2001c, 2001d, 2001e, 2001f, 2001g, 2001h). Moreover, the rice genome is relatively small (430 Mbp), which facilitates map-based cloning of novel genes (Song et al. 1995) and sequencing of the entire genome. For the past several years, a consortium of 10 countries led by Japan has been sequencing the rice genome (Anonymous 2001h). In April 2000, Monsanto announced that a rough draft of the entire rice genome had been completed (Anonymous 2001i), and that the data will be made available for public use through the international consortium (Barry 2001). The full genome sequence will stimulate public research, including research on dormancy in rice and related species.

There are some disadvantages to using rice as a system to clone dormancy genes. Rice is a large plant with a long generation time. It can take 6 mo or more to produce mature rice seeds for dormancy investigations. The nondomesticated strains that possess high levels of dormancy have undesirable traits in the greenhouse like photoperiod sensitivity, tillering, long awns, and seed shattering. However, these weedy or wild-like strains are essential for developing segregating populations with great differences in germinability and high levels of genetic polymorphism. Some of the weedy or wild-like strains are closely related to Asian wild rice (*Oryza rufipogon*), a wild progenitor to cultivated rice, and they carry alleles that impart relatively high levels of dormancy (Cho et al. 1995). High levels of polymorphism aid in constructing genetic linkage maps, in conducting QTL analysis, and ultimately in cloning QTL. Tanksley and his colleagues at Cornell University cloned the first plant QTL using a map-based approach (Frary et al. 2000). Their papers provide insight into using nondomesticated tomato species (*Lycopersicon* spp.) to enhance phenotypic differences, developing near-isogenic lines to facilitate Mendelian resolution of a quantitative trait, and cloning a major gene that controls tomato fruit size (Alpert and Tanksley 1996; Alpert et al. 1995).

Three groups have reported dormancy QTL for rice (Cai and Morishima 2000; Lin et al. 1998; Wan et al. 1997). Two of the three populations used for these analyses were derived from domesticated cultivars that either had unknown levels of germinability or low levels of dormancy. Therefore, usefulness of these populations for map-based cloning of dormancy genes is unknown or questionable. The third population used to examine dormancy QTL in rice might be more useful because a dormant strain of Asian wild rice was used as a parent and the researchers considered differences in germinability due to the hull and pericarp/testa (Cai and Morishima 2000).

Potato and Sorghum

Dormancy in potato tubers (*Solanum tuberosum* L.) has been investigated to reduce postharvest losses during storage. The untimely release of dormancy that results in sprouting and changes in the chemical composition of the tuber reduces market quality. Two groups have conducted QTL analysis of potato tuber dormancy. Freyre et al. (1994) de-

veloped a segregating population from the cross (*S. tuberosum* × *S. chacoense*) × *S. phureja*. They developed a genetic linkage map and conducted QTL analyses that identified six QTL associated with dormancy. A multilocus model that takes into account epistatic interactions explained about 72% of the phenotypic variation for dormancy in their population. van den Berg et al. (1996) conducted similar analyses using reciprocal backcrosses between *S. tuberosum* and *S. berthaultii* and detected QTL on nine chromosomes. Alleles from the wild parent (*S. berthaultii*) promoted dormancy. Several of the QTL found in the two investigations appear similar based on their chromosomal positions.

Another method to investigate dormancy in potato tubers might be through microarray analysis. Microarray analysis can provide genome-scale information about gene expression patterns related to the phenotype under investigation, e.g., dormancy and nondormancy (Chao 2002). Expressed sequence tags (ESTs) and microarray chip production is progressing or is being considered for most economically important crops (Anonymous 2001j; Richmond and Somerville 2000). For example, the Institute for Genomic Research (TIGR) is developing 60,000 ESTs for potato and was requesting orders for their 1,000-element microarray chips (Anonymous 2001k). Perhaps these microarray chips could be employed to investigate vegetative reproduction in related species like horsetail or dormancy in tubers of perennial weeds like Jerusalem artichoke.

Grain sorghum is an important cereal grain in some arid parts of the world and it has a relatively small nuclear genome size (750 Mbp) in relation to corn or maize (*Zea mays* L., 2,500 Mbp), oat and wild oat (11,000 Mbp), and wheat, (16,000 Mbp) (Arumuganathan and Earle 1991). Like other economically important plants with relatively small genomes, many genetic resources are publically available (Anonymous 2001l, 2001m). Although grain sorghum does not reproduce vegetatively, the closely related species *Sorghum propinquum* (Kunth.) Hitchc. is a rhizomatous perennial weed native to South Asia. The rhizomatous perennial weed johnsongrass is an interspecific hybrid descendant of *S. bicolor* and *S. propinquum*. Paterson et al. (1995a) crossed the aforementioned species to develop populations segregating for seed shattering, tillering, and rhizomatous growth. Using these populations and molecular genetic techniques, they conducted QTL analysis and marked three QTL for rhizome production. The QTL accounted for only 22% of the phenotypic variation in number of rhizomes producing aboveground shoots, with the strongest QTL accounting for 13% of the variation. Map-based cloning of this QTL may not be possible because of the size of the sorghum genome and the lack of a QTL that accounts for a greater percentage of the phenotypic variation. Thus, microarray analysis might be used to complement the QTL analysis or to seek independently additional genes that play a role in the growth and development of rhizomes. Microarray analysis will be facilitated by the 67,000 publically available sorghum ESTs (Anonymous 2001n).

Weeds for Dormancy Investigations

Wild Oat, Rice, and Orthologous Loci

When considering a weed for fundamental investigations of dormancy, its biological attributes should be carefully

considered in relation to the hypothesis or question being tested. For example, QTL analysis and map-based cloning might not be the best approach for identifying genes regulating dormancy in leafy spurge underground adventitious buds, e.g., crown and root buds (see Chao 2002) because leafy spurge is genetically complex, its mating system is poorly characterized and few genetic resources and tools are available. On the other hand, microarray analysis using ESTs from leafy spurge or a related crop species is feasible (Horvath and Anderson 2002) and has the potential for discovering a limited number of marker genes or many genes expressed during bud growth and development (Richmond and Somerville 2000). Variables to consider in the selection of suitable weeds for dormancy investigations are the relationship of the weed to the crop species, genome size, mating system, and genetic constitution, e.g., ploidy.

Wild oat is a serious weed worldwide in small grain cropping systems (Holm et al. 1977). There has been more descriptive and mechanistic research done on coat- and embryo-imposed seed dormancy in wild oat than in any other species (Simpson 1990). From that perspective and its close relationship with the cultivated oat, wild oat is an excellent system for dormancy investigations. Unfortunately, wild oat is a hexaploid with much repetitive DNA and a large genome size (11,000 Mbp), and is therefore not suited for map-based cloning of dormancy genes. In contrast, rice is a diploid with a small genome and it displays various types of seed dormancy. Many scientists believe that rapid strides in understanding dormancy in cereal grain species will require map-based cloning of genes that directly regulate germinability of rice. The rationale for using rice as the vehicle to clone dormancy genes from wild oat is based on research in the area of comparative genetics. It has been demonstrated that gene content, order, and to some extent function, are highly conserved and colinear between different species within the grass family (Devos and Gale 1997). Using the 12 chromosomes of rice as the reference genome, the genetic maps of rice, foxtail millet, sugarcane (*Saccharum officinarum* L.), sorghum, maize, wheat, barley (*Hordeum vulgare* L.), and oat were integrated by Devos and Gale (1997). Several important concepts have emerged from this effort, in particular the concept of orthologous loci. This term refers to the idea that genes arising from a common ancestor are conserved in different species. For example, genes for seed shattering, red grain color, and plant height are conserved and colinear across several cereal genomes (Devos and Gale 1997; Paterson et al. 1995b). When QTL that regulate germinability of rice directly are cloned, these genes could be used to probe segregating wild oat populations to test the hypothesis that orthologous loci regulate dormancy in wild oat. Because there have been few efforts aimed at developing rice as a system to clone dormancy genes, domesticated and nondomesticated rice germplasms are being screened for levels and types of dormancy, and crosses will be made based on the extreme variation in germinability found in different cultivars and nondomesticated strains (Gu and Foley 2001).

Dormancy genes from the dicot *Arabidopsis* could also be used to probe for dormancy genes in wild oat. However, comparative information is less useful across more distantly related taxa in which gene function diverged over time. Grasses have diverged from one another for less than 66

million years, whereas monocots and dicots diverged 120 to 200 million yr ago (Paterson et al. 1996, 2000). Nevertheless, dormancy genes in *Arabidopsis* might be used to probe for orthologous loci in other members of the family Brassicaceae like wild mustard, a serious weed whose seeds after-ripen under the same conditions as *Arabidopsis* (Buhler and Hoffman 1999).

Foxtail Species

Dormancy in foxtail species has been studied for many years (Dekker et al. 1996; Simpson 1990). Seeds of foxtail species after-ripen under cool, moist conditions; this is different from wild oat and rice, which normally after-ripen under warm, dry conditions. Foxtail millet is a crop with a breeding system that is conducive to genetic investigations (Wang et al. 1998). Foxtail millet and green foxtail are closely related species that can be cross-pollinated (Devos and Gale 1997; Li et al. 1998). If researchers screened domesticated and nondomesticated strains of foxtail species for extreme differences in germinability, made crosses, and developed segregating populations, it may be feasible to use a map-based procedure to clone genes that regulate dormancy in foxtail species.

Jointed Goatgrass

Wheat is under intense investigation and many genetic stocks are available for research because it is an important food crop. As with rice, wheat breeders are interested in genes that impart low and predictable levels of dormancy to obtain resistance to preharvest sprouting. Jointed goatgrass is a weed with significant levels of seed dormancy. Wheat and jointed goatgrass are similar because they share a common ancestor, the donor of the D genome (Zemetra et al. 1998). An EST database for wheat is being developed (Anonymous 2001a) and 24,346 entries were generated in Phase I of the project. Walker-Simmons et al. (2001) used this database and microarray analysis to investigate resistance to preharvest sprouting in wheat. These resources might be used to examine dormancy in jointed goatgrass. An important outcome of understanding seed dormancy in jointed goatgrass might be solving the problem of preharvest sprouting in wheat. For example, if phenotypic differences in germinability of wheat and jointed goatgrass are determined to be due to allelic variation in orthologous loci or even different loci, perhaps these alleles or genes from *Aegilops* spp. could be introgressed into wheat to reduce losses caused by preharvest sprouting (Lan et al. 1997).

Leafy Spurge

Leafy spurge is an important perennial weed in the Northern Plains of the United States and Canada. The growth and development of crown and root buds has been described, but little information is available on genes regulating dormancy mechanisms, signals, and pathways. Horvath and Anderson (2002) have taken a three-pronged genomics approach to examining dormancy in leafy spurge root buds. First, they isolated approximately 1,000 ESTs from a cDNA library constructed from leafy spurge root buds and created leafy spurge DNA microarray chips to investigate the growth and development of leafy spurge crown and root

buds (Anderson and Horvath 2001; Anonymous 2001j). Constructing an EST database for microarray analysis is expensive, time consuming, and requires considerable resources for bioinformatics. Therefore, they are collaborating with scientists conducting research on cassava (*Manihot esculenta* Crantz) to develop an EST database to investigate postharvest storage of tubers and disease resistance. Cassava is a food crop, and like leafy spurge, a member of the family Euphorbiaceae. Hence, resources developed for cassava may aid in efforts to investigate dormancy in leafy spurge. These researchers demonstrated that about 68% of Arabidopsis DNA on a microarray chip hybridized with cDNA from mature leaves and meristems of leafy spurge (Horvath and Anderson 2002). This level of hybridization should be sufficient to survey for genes and gene families that are up- and down-regulated in root buds depending on their stage of growth and development. However, despite the likelihood of gaining extraordinary insights, Arabidopsis is not a perennial, and it cannot be used to address every aspect of plant growth, development, and reproduction (Yuan et al. 2001). Therefore, it may be prudent to move forward with the development of an EST database for leafy spurge or another perennial with underground adventitious buds.

Canada Thistle

Canada thistle is a serious weed of much of the United States and Canada that expresses strong vegetative reproduction by means of adventitious root buds on its extensive root system (Donald 1994). Canada thistle is in the family Asteraceae, which contains important crops like lettuce (*Lactuca sativa* L.) and sunflower (*Helianthus annuus* L.). Research groups interested in these crops are undertaking a Compositae Genome Initiative (Anonymous 2001j, 2001p). If developed, perhaps the Compositae EST database could be used to develop Canada thistle as a system for investigating dormancy in adventitious, underground buds or applied to investigate vegetative reproduction in weeds more closely related to lettuce and sunflower, e.g., prickly lettuce and Jerusalem artichoke.

Purple and Yellow Nutsedge

Purple and yellow nutsedge are two of the world's worst weeds (Holm et al. 1977). Reproduction and spread of these weeds is largely ascribed to tubers, and control is difficult because of the survival of numerous dormant tubers in the soil (Neeser et al. 1997). Unfortunately, the family Cyperaceae has few important crops for which genetic resources might be developed that may be used to investigate dormancy in nutsedge tubers. Therefore, microarray analysis of dormancy in nutsedge tubers might rely on potato DNA microarrays hybridized with nutsedge cDNA in the same way Arabidopsis DNA microarrays have been used to examine gene expression in a number of unrelated species (Horvath and Anderson 2002).

Approximately 250 species of flowering plants are considered serious weeds (Holm et al. 1977). Of these weeds, molecular genetic and genomic approaches have been applied to investigate dormancy in johnsongrass, weedy rice, wild oat, and leafy spurge. Other than the aforementioned weeds, most weeds have had no effort devoted to fundamental investigations of dormancy. Given the importance of dormancy

in the persistence and spread of weeds, it is going to take many more researchers with good ideas and skills to develop knowledge on dormancy that can be applied to solve problems in weed management. Unfortunately, the resources available to the weed science community are often more limited than the resources available to other plant and crop scientists. Nevertheless, many existing and developing resources for crop and model plant systems can be adapted or further developed to investigate dormancy in weedy species. With the creative use of resources available in the 21st century, opportunities will expand to elucidate the fundamental basis for dormancy in weed seeds and vegetative propagules.

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